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Temporal and Spatial Interactions between Coyotes and Red Foxes along the Urban-Rural Interface

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Temporal and Spatial Interactions between Coyotes and Red Foxes along the Urban-Rural Interface

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By

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Intraguild competition between predators may cause one predator to alter their temporal activity patterns or occupancy to reduce competition or avoid aggressive encounters. I conducted a temporal activity pattern and occupancy study of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in and around Lincoln, Nebraska using camera traps deployed from September of 2020 to May of 2021. I evaluated the activity patterns of coyotes, red foxes, and humans in urban and rural settings along with the activity patterns of red foxes when sympatric or allopatric with coyotes and determined the coefficient of overlap (Δ) between these various groups using kernel density estimators. I found that coyotes avoid humans temporally more intensely at rural sites (Δ_1 = 0.157, 95% CI: 0.078 – 0.244) than at urban sites (Δ_1 = 0.446, 95% CI: 0.335 – 0.570). Coyotes and red foxes that were sympatric did not show statistically significant differences in activity patterns with a Δ_1 = 0.689 (0.433 – 0.898, WT $P > 0.10$). Red foxes did not show statistically significant difference in activity patterns when sympatric or allopatric with coyotes with a Δ_1 = 0.745 (0.528 – 0.926, WT $P > 0.10$). I used a single species model to evaluate factors influencing red fox occupancy. The urban model was most informative with ß = 9.85 (-52.09 – 71.8) for the urban covariate. Probability of red fox occupancy of an urban site was 0.785 (SE = 0.16) while just 0.0002 (SE = 0.006) for rural sites. This model paired with only four captures of rural red foxes and nine captures of red foxes sympatric with coyotes would suggest that spatial avoidance is more important than temporal avoidance in this system. However, future research

should attempt to obtain more detections of both species at sites where they do coexist, as these areas may provide important insight into potential temporal niche partitioning between red foxes and coyotes across this urban-rural gradient.

Acknowledgments

I thank N. Wehr, A. Oetting, and all students in the SNR Mammalogy classes in 2019 and 2020 for participating with fieldwork. I thank E. Hubbs at Spring Creek Prairie, D. Wedin at 9-Mile Prairie for allowing us camera trap on these properties. I thank B. Zink for allowing us to camera trap on his private property. I thank Nebraska Game and Parks, Lincoln Parks and Recreation, Waverly Parks and Recreation, and Seward Parks and Recreation for allowing us to camera trap on their properties. I thank D. Ferraro and the Nebraska Cooperative Fish and Wildlife Research Unit for providing cameras. I thank J. Benson and D. Dougherty for their extensive guidance and support throughout the entire thesis process.

Contents

Introduction

Competition is a central component of ecological understanding and, at its core, is one of the most important factors in the ecology and evolution of a species (Wilson 2014). Species can compete either through interference or exploitation with interference competition referring to scenarios where two species or individuals interact directly in a manner that limits the ability of one or both to use a resource (Tajima et al. 2019). When species engage in exploitative competition, they limit the other's use of a resource indirectly, through shared use of the same resource (Culbertson and Herrmann 2019; Tynkkynen et al. 2006).

When species compete, the two possible outcomes are competitive exclusion and niche partitioning. In competitive exclusion there is a "winner" and a "loser", meaning one species will outcompete the other, and the loser will either be driven to extinction. Niche partitioning refers to one or both of the competing species making adjustments to their diet, habitat use, occupancy, or temporal activity to reduce competition (Carothers and Jaksić 1984; D'Andrea et al. 2020; Di Bitetti et al. 2009). Thus, studying temporal activity patterns of potentially competing species can provide evidence of temporal niche partitioning.

It is well established in ecology that prey species employ strategies to avoid predation through temporal, spatial, or other behavioral means (Atickem et al. 2014, Hebblewhite and Merrill 2009, Higdon et al. 2019). This avoidance of perceived predation risk has been described as the "landscape of fear" (Brown and Kotler 2005; Laundré et al. 2001). Traditionally, the landscape of fear concept revolved around the idea that animals perceive predation risk as constant in time, such that spatial avoidance was the key behavioral response to reduce risk (Lima 2002). This can lead to important forage-predation risk tradeoffs whereby prey potentially

avoid areas where predation risk was high, even if these areas provided forage opportunity. Recent studies have shown that predation risk is not constant in time and recognize that the landscape of fear can be temporally dynamic (Kohl et al. 2018). As such, prey may be able to use potentially risky areas at relatively safer times when predators are inactive, thereby allowing them to access profitable foraging sites while still minimizing predation risk (Kohl et al. 2018). Competing carnivores prone to dangerous encounters for the smaller species may exhibit similar patterns in time and space as predators and prey.

Additionally, predator species will often avoid areas of human presence (Hebblewhite and Merrill 2008, Nickel et al. 2020, Ordiz et al. 2011). Recognizing this phenomenon, Berger (2007) described the human shield hypothesis whereby prey species may use the presence of humans to shield themselves from the risk of predation. Competition between carnivores is common, and intraspecific killing occurs between some species (Fedriania et al. 2000, Palomares and Caro 1999). Predator-prey interactions described by the landscape of fear and human shield hypotheses may also apply to intraguild interactions between carnivores involved in interference competition. Larger predators often avoid humans temporally by shifting to be active primarily during nocturnal periods in areas where human activity is common (e.g., Frey et al. 2020). Thus, in human-dominated landscapes, it makes sense that smaller canids might become more diurnal in areas of high human activity to avoid risky encounters with larger canids that might be strongly crepuscular or nocturnal. Such behavior would represent a “temporal human shield” between competing carnivores.

The effects of human activity on intraguild interactions of species that bridge the urban and rural interface are poorly understood. Additionally, it is unclear how human presence influences two populations of the same species in urban and rural environments in close

proximity. However, studies addressing this question may add to the collective understanding of behavioral variation relative to gradients of anthropogenic disturbance. Coyotes have greatly expanded their historical range since the 1900s and have adapted well to living in and alongside human-dominated environments (Gese et al. 2012, Poessel et al. 2016). Foxes have also shown an ability to thrive in areas of intense human use (Gosselink et al. 2003, Mueller et al. 2018). Studying variation in the behavioral responses of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in urban and rural settings with otherwise similar environmental conditions provides a powerful study system for evaluating plasticity in behavior for these highly adaptable species.

Coyotes and the smaller red foxes often utilize similar prey and habitats, which leads to red foxes being harassed and occasionally killed by coyotes to reduce competition (Mueller et al. 2018; Palomares and Caro 1999, Sargeant et al. 1998). In response, foxes often avoid areas used by coyotes which can contribute to reduced density in settings where both species occur (Cypher 1993, Gosselink et al. 2003, Lombardi et al. 2017, Mueller et al. 2018, Sargeant et al. 1998, Voight and Earle 1983). In Illinois, coyote predation had largely replaced hunting as a major cause of mortality for rural red foxes, whereas no red foxes were killed by coyotes in adjacent urban areas (Gossselink et al. 2007). Thus, spatial avoidance of coyotes by red foxes occupying urban areas may reduce competition with coyotes (Gosselink et al. 2007, Mueller et al. 2018). However, coyotes and red foxes are sympatric in some cities, suggesting that red foxes may also need to employ temporal avoidance to reduce competition as both species are generally crepuscular or nocturnal across their ranges (Baker et al. 2007, Frey et al. 2020). Thus, red foxes might strongly avoid coyotes in space, or they may be able to occupy these risky places by shifting activity to avoid coyotes in time.

Lincoln, Nebraska represents an opportunity to study coyotes and red foxes in time and space along an urban-rural interface. Perception of increased numbers of coyotes and red foxes in Lincoln in recent years has encouraged considerable interest in these two species. A better understanding of the behavior of urban canids relative to humans would inform managers as they tackle questions and concerns of residents living alongside coyotes and red foxes Coyotes and red foxes live in and around Lincoln ranging from urban areas to rural locations outside of city limits. This combination of coyote and red fox presence within developed and agricultural spaces facilitates asking questions about how varying degrees of human activity might influence spatiotemporal interactions between competing canids. Identifying whether coyotes are influenced by human activity in urban areas - and if foxes are taking advantage of this pressure - will help determine whether the human shield and landscape of fear can be extended to intraguild interactions in both time and space.

I investigated temporal activity patterns and site occupancy of coyotes and red foxes across varying levels of human disturbance in and adjacent to Lincoln, Nebraska. I hypothesized that smaller predators should avoid larger predators in either space or time. Specifically, I predicted that urban coyotes would be less active during the day compared to rural coyotes given the greater human activity within the city. Next, I predicted occupancy of red foxes would be negatively influenced by coyote occupancy. I also predicted that in areas where red foxes and coyotes are sympatric, red foxes would exhibit temporal avoidance to reduce overlap in activity patterns with coyotes, whereas in areas where coyotes are absent red foxes would be “freed” from the need to avoid coyotes in time.

My second hypothesis extends the human-shield concept from a purely spatial process to one that operates in both space and time. Specifically, I hypothesized that smaller predators can

use human activity and infrastructure as a shield from larger predators in both space and time, given the tendency of large predators to strongly avoid humans. Specifically, I predicted that red fox occupancy would be positively influenced by development and human activity and (as stated above) negatively influenced by coyote occupancy. Second, I predicted coyotes would strongly avoid human activity temporally. Last, I predicted that red foxes would avoid humans temporally more strongly in areas that are not occupied by coyotes. This work will contribute to a better understanding of the role played by humans in mediating temporal and spatial interactions of red foxes and coyotes in urban and rural areas. Given the potential for human-carnivore conflict in urban areas, understanding how interactions between coyotes and red foxes are influenced by human activity and infrastructure will be vital for creating effective management plans.

STUDY AREA

I studied coyotes and red foxes in and around the city of Lincoln, Nebraska. Lincoln was a city of over 250,000 people surrounded by suburban and rural areas (U.S. Census Bureau 2010). Land use ranged from fully urban areas to agricultural fields. Urban areas were dominated by roads, commercial areas, and residential development with interspersed developed open spaces like large city parks, golf courses, and maintained riparian corridors. Rural areas were dominated by agriculture, but many rural camera sites were placed in Audubon centers, state recreation areas, or wildlife management areas comprised of tallgrass prairie, other grasslands, and forested patches. Local mammals included but were not limited to white tailed deer (*Odocoileus virginianus*), lagomorphs (family *Leporidae*), squirrels (*Sciurus niger*), raccoons (*Procyon lotor*), and a large number of domestic dogs (*Canis lupus familiaris*).

METHODS

Field Methods

We set up cameras in and around Lincoln, Nebraska with roughly half of the cameras in urban areas and half cameras in rural areas (Fig. 1). We found natural settings to place the camera traps to keep sites similar across urban and rural locations. We placed attractants at each camera trap and revisited camera traps every two to three weeks. To ensure independence between sites (i.e. minimize capturing the same red foxes at multiple cameras), we separated cameras by at least 1960m. This distance corresponded to the radius of mean red fox home range size in Lincoln, Nebraska and elsewhere (Šálek et al. 2015, Dougherty 2019). I based the camera spacing distance on the home range size of the smaller of the two focal species (red foxes) for greater resolution.

We deployed camera traps using two different approaches given that our camera trap data were used to address multiple research objectives. In the spatial occupancy and temporal activity design, we placed camera traps on trees at a height of 0.4-1.5 meters. We applied Reuwsaat's Private Stock Fox Pure Urine (Reuwsaat's Extreme Performance Baits & Lures, South Dakota) roughly three meters away from the camera as an attractant. We set the cameras to take motion triggered still photographs as still photographs were adequate to identify animals captured on camera and extended the battery life of our camera trap deployments. Each photograph had a time stamp recorded with each capture.

Our data was supplemented by camera data we collected for a coyote boldness study done from September of 2021 to January of 2021. For this coyote boldness study, we set cameras to take 30 second videos with a 5 second delay period (Breck et al. 2019). For each video, we recorded the time stamp at which the animal first appeared in frame. Camera trap locations were

baited with a large tablespoon of Sweet Meat Predator Bait (Russ Carman, New Milford, Pennsylvania) covered with leaf litter and a fatty acid tab (Pocatello Supply Depot, Idaho) placed on top (Breck et al. 2019). As part of this study, we placed a novel object at some of the camera trap sites. The novel object was 4 stakes made of processed wood placed one meter apart in a square. A piece of rope was tied around the top of the stakes (Breck et al. 2019). Although individual animals may have reacted differently to the presence of the novel object, and this could have biased occupancy analysis, we do not think it affected our ability to study temporal activity patterns of red foxes and coyotes. Thus, we only used detections collected with video data for the temporal activity patterns and excluded it from the occupancy analysis. We also supplemented camera data with 2019 camera trap data collected at Spring Creek Audubon Center southwest of Lincoln, Nebraska. This location was also used during this study.

Temporal Activity Patterns

To determine shifts in activity patterns, I measured the coefficient of overlap (Δ) for 9 groups: (1) coyotes in urban and rural settings, (2) red foxes in urban and rural settings, (3) humans in urban and rural settings, (4) humans and coyotes in urban settings, (5) humans and coyotes in rural settings, (6) humans and red foxes in urban settings, (7) humans and red foxes in rural settings, (8) sympatric red foxes and coyotes, and (9) red foxes sympatric and allopatric with coyotes. The coefficient of overlap utilizes a kernel density estimator to estimate temporal activity patterns. Coefficients of overlap range between zero (no overlap) and one (total overlap of activity patterns;Ridout and Linkie 2009). I used the Δ_1 estimator for all groups as samples sizes of urban coyotes, rural coyotes, rural foxes, and foxes sympatric with coyotes were all <75 captures (Meredith and Ridout 2017). I created 95% confidence intervals around these

coefficients of overlap by bootstrapping with 1,000 iterations. I used the package "overlap" in R version 4.0.4 (R Core Development Team 2020) for all temporal activity analysis.

In addition to the coefficient of overlap, I used the Rao's spacing test of uniformity (RST) and Watson's two-sample test of homogeneity (WT). I used Rao's spacing test of uniformity to determine whether an activity pattern was statistically different from a uniform distribution. I used Watson's two sample test of homogeneity to determine whether two activity patterns were statistically different enough to be considered non-homogenous. The Rao's spacing test of uniformity and Watson's two-sample test of homogeneity both used the package "circular" in R (Monette et al. 2020).

Occupancy

I measured occupancy by recording whether or not red foxes or coyotes were captured at each camera site. We left cameras on the landscape, but camera data were split into week long sampling periods. Each camera would receive scores of 1 or 0 depending on if a coyote or red fox had been captured at that location that week (Santos et al. 2019). I used the package "unmarked" in R to fit single species single season occupancy models (Mackenzie et al. 2002,). I fit a global model to evaluate the effects of urban versus rural areas and coyote presence or absence on red fox occupancy using dummy coded variables for urban (reference: rural) and coyote presence (reference: coyotes absent at site). I then fit a null model and univariate models with each dummy coded covariate and ranked the four models using the Akaike information criterion correction for small sample size (AICc, Burnham and Anderson 2003).

Results

Temporal Activity Patterns

I obtained 90 camera detections of coyotes (45 at urban sites, 45 at rural sites) along with 80 camera detections of red foxes (76 at urban sites, 4 at rural sites). Additionally, I obtained 640 captures of humans (484 at urban sites, 156 at rural sites).

Rural coyote activity was crepuscular/nocturnal with coyote activity rising at about 06:00 hours, decreasing during the day, and peaking just before midnight (24:00 hours) (RST $P < 0.001$). Urban coyote activity peaked first in the early morning (02:00 hours) before peaking again in the morning around 10:00 hours (RST $P > 0.10$). Urban and rural coyote activity overlapped during crepuscular and nocturnal periods ($\Delta_1 = 0.609$, 95% CI: 0.464 – 0.734, WT $0.001 < P < 0.01$; Fig. 2).

Red fox activity at urban sites was crepuscular with peaks at 06:00 hours and 20:00 hours (RST $P > 0.10$). Red fox activity patterns at rural sites were also crepuscular with a peak before 04:00 hours and 18:00 hours. The sample size of rural red foxes was only 4 detections, which limited power to reject that this distribution was uniform (RST $P > 0.10$). The Δ_1 for urban and rural red foxes was 0.305 (95% CI: 0.127 – 0.560, WT $P > 0.1$; Fig. 3).

Human activity patterns were very similar across urban and rural sites, but urban humans did have a later peak in activity. Rural humans had an activity peak after 12:00 (RST $P < 0.001$) while urban humans peaked later in the afternoon (15:00 hours; RST $P < 0.001$). Both were rarely active after sunset (Fig. 4). Urban and rural humans had a Δ_1 of 0.772 (95% CI: 0.699 – 0.846, WT $P < 0.001$).

Humans overlapped with coyotes and red foxes at similar rates. Humans and coyotes at urban sites had a Δ_1 of 0.446 (95% CI 0.336 – 0.556, WT $P < 0.001$; Fig. 5). Humans and red

foxes at urban sites had a Δ_1 of 0.426 (95% CI: 0.326 – 0.516, WT $P < 0.001$; Fig. 6). Rural humans and coyotes had a Δ_1 of 0.157 (95% CI: 0.081 – 0.242, WT $P < 0.001$; Fig. 7). Rural humans and foxes however had a similar Δ_1 at 0.149 (95% CI: 0.017 – 0.304, WT $0.01 < P < 0.05$; Fig. 8).

Red foxes captured at camera sites where they co-occurred with coyotes had activity patterns peaking before 04:00 hours, in the afternoon (15:00 hours), and in the evening (20:00 hours; $P > 0.10$). A sample size of only 9 detections of red foxes in sites occupied by coyotes did not provide much power to evaluate whether their activity patterns differed from a uniform distribution (RST $P > 0.10$). Red foxes captured at camera sites where coyotes were not detected had activity patterns peaking at 06:00 hours and 19:00 hours (RST $0.01 < P < 0.05$). Red foxes at sites where coyotes were and were not detected had a Δ_1 of 0.745 (95% CI 0.533 – 0.910, WT $P > 0.10$; Fig. 9).

Coyotes captured at camera sites where red foxes were also detected had temporal activity patterns peaking in the early morning (04:00 hours) and again just before midnight (23:30 hours; RST $0.001 < P < 0.01$). Coyotes and red foxes captured at the same sites had a Δ_1 of 0.689 (95% CI: 0.444 – 0.899, WT $P > 0.1$; Fig. 10).

Red foxes that were sympatric with coyotes had a Δ_1 with humans of 0.378 (95% CI: 0.135 – 0.617, WT $0.001 < P < 0.01$). Red foxes detected at sites where coyotes were not detected had a Δ_1 with humans of 0.418 (95% CI: 0.332 – 0.504, WT $P < 0.001$).

Occupancy

The only strongly supported model of red fox occupancy retained the single variable of urban and was superior to the global model with urban and coyote presence (ΔAICc = 3.2), the null model (ΔAICc = 6.5), and the model with only coyote presence (ΔAICc = 7.2; Table 1).

However, there was considerable uncertainty associated with the variable of urban retained in the top model ($\beta = 9.9$, 95% CI= -52.1 to 71.8). Despite this uncertainty, the top model predicted that probability of red fox occupancy was 0.79 (SE = 0.16) in urban sites, whereas the probability of red fox occupancy was < 0.01 (SE = 0.006) in rural sites.

Discussion

Rural coyotes appeared to avoid temporal overlap with humans more intensely than urban coyotes. This result was limited by small sample size, but there are still credible inferences to be made. A potential cause of this unexpected result is that coyotes may have different interactions with humans in urban and rural settings. Coyotes are likely persecuted (e.g., by shooting and trapping) more aggressively by humans in rural settings than they are in urban settings. Urban coyotes spend their time completely surrounded by people and are possibly more acclimated to a human presence (Mccleery 2009).Most interactions between humans and coyotes in an urban setting probably do not result in injury or potential mortality for coyotes as evident by the 86 coyote calls to Lincoln animal control between June and September of 2020 (Fig. 11;K. Dougherty, personal communication, 19 April 2021). This could factor into rural coyote adherence to a crepuscular/nocturnal activity pattern. While urban coyotes still avoid humans as the data suggests, they may be more tolerant of potential encounters because the consequences are less severe than for rural coyotes (Timm and Baker 2007). These results supported my prediction that coyotes would avoid humans in time but did not support my prediction that urban coyotes would be less active during the day.

My second prediction stated that occupancy of red foxes would be negatively influenced by coyote occupancy. This prediction was not supported by the data as the model with coyote presence as a covariate was not more informative than the model including urban/rural as a

predictor of red fox occupancy. While I captured an even split of coyotes between urban and rural sites, there were only four captures of red foxes at rural camera traps (Fig. 12). This would suggest that human development was the most important factor influencing red fox occupancy. This is consistent with red fox selection of urban spaces described in Mueller et al. (2018). While coyote occupancy was not the best predictor of red fox occupancy with these data, coyotes have been known to harass foxes and negatively impact occupancy (Cypher 1993, Gosselink et al. 2007, Lombardi et al. 2017). It is possible that with more data, the same coyote presence would have a stronger, negative influence on red fox occupancy. It is worth noting that there were very few instances of red foxes being captured at sites where coyotes were also captured (n = 9) and that the second best occupancy model retained the negative influence of coyote presence (Table 1).

The data also did not support my third prediction that red foxes sympatric with coyotes would exhibit temporal avoidance to reduce overlap in activity patterns with coyotes. There was no evidence that being sympatric with coyotes affected red fox temporal activity patterns. The lack of detections of both species at the same sites suggests that red foxes may strongly avoid coyotes spatially in and around Lincoln. Consistent results were found using telemetry data of red foxes and coyotes in similarly sized Madison, Wisconsin (Mueller et al. 2018). Red foxes would not need to avoid coyotes in time if they are already spatially separated. This would be more consistent with the original understanding of the landscape of fear (Brown and Kotler 2005, Higdon et al. 2019, Laundré et al. 2001). More time would be needed in the few places of red fox and coyote co-occurrence to investigate the potential for intraguild temporal interactions. Additionally, it is possible that red foxes or coyotes were present at some sites but that I failed to detect them.

The urban model of red fox occupancy made predictions consistent with the human shield hypothesis described by Berger (2007) and Hebblewhite and Merril (2008, 2009) and was consistent with my hypothesis. While unable to draw strong conclusions due to low statistical power, the occupancy model did predict trends that supported my first prediction that human activity and development would be a positive influence on red fox occupancy. The urban covariate model was the most informative for red foxes and predicted that for any given urban site, there was a 79% chance that a fox was occupying it. This occupancy probability was less than 1% for rural locations. Red foxes showed a higher probability of occupying urban sites, which could be due to red foxes utilizing the human shield against coyotes (Gosselink 2003,2007).

The data did not support my last prediction that red foxes would avoid humans temporally more strongly in areas that were not occupied by coyotes. Red foxes sympatric with coyotes did not avoid humans more strongly than red foxes in areas where coyotes were not detected, and red foxes and coyotes temporally avoided humans at similar rates at urban and rural sites. Making comparisons with activity patterns of red foxes co-occurring with coyotes proved challenging because detections in the same sites were rare. More data is needed from locations where red foxes and coyotes are sympatric to understand whether intraguild competition is leading to changes in activity patterns.

While many of my analyses did not have large enough sample sizes to provide definitive results, they did suggest trends that make biological sense. The small sample sizes were particularly challenging when doing occupancy modeling as power was often too low to make strong predictions. Power issues aside, the urban model still made predictions consistent with studies that also looked at foxes in urban areas (Dougherty 2019, Gosselink et al. 2007,

Lombardi et al. 2017, Mueller et al. 2018). Expanding the camera grid and maintaining camera traps on the landscape for longer monitoring periods would help to remedy these power issues.

The urban versus rural binary choice was also an area future studies in this system could improve upon. Characterizing urban and rural sites can be subjective and difficult to measure on the landscape. The urban-rural interface is too variable to measure with a binary choice. Quantifying density of development at sites might be more informative and mitigate ambiguity associated with classifying sites as either urban or rural. Similar uses of distance to development metric are common in resource selection modeling (Benson 2016, Hollis-Etter et al. 2019). This finer measurement would allow for a clearer picture of how these animals are interacting with the landscape.

Future studies should also consider tracking coyotes and red foxes with telemetry within this study system. While red foxes in Lincoln have already been tracked using Global Positioning System collars, coyotes and red foxes have never been tracked together in this system (Dougherty, 2019). Telemetry data would allow the analysis of spatial patterns at a finer scale than is possible with just cameras. Understanding how a coyote moves across the urban landscape may help explain why there is less adherence to a crepuscular activity pattern than there was for rural coyotes. Mueller et al. (2018) was very successful in using telemetry to answer many of the questions I aimed to tackle here.

A final suggestion for extended study would be to obtain abundance estimates of each species. Estimating how many of each species are found in and around Lincoln could benefit the understanding of how these species avoid each other in space. It would be my prediction that there are more red foxes within city limits than outside, and vice versa for coyotes. Use of time to event or space to event methods of estimating abundance would take advantage of the camera

trap studies already taking place (Loonam et al. 2021, Moeller et al. 2018). Considerations would need to be made for the nonrandom locations of the current camera grid. A time to event study would also need estimates of movement speed which would be an added benefit of collecting telemetry data (Loonam et al. 2021, Moeller et al. 2018).

There is no doubt that coyotes are present in Lincoln, and their departure from a strict crepuscular activity pattern has interesting management implications. This would suggest that coyotes could be becoming habituated to human activity. When coyotes become habituated, there is potential for an increase in human-wildlife conflict (Timm and Baker 2007). If coyotes are going to be present in urban areas, it is important to keep them fearful of people. Suggestions have already been made by local authorities educating the public to throw rocks, yell, or use sticks to scare off coyotes (Salter 2020). An understanding of where and when these animals are active will also be helpful in cases where specific actions must be taken.

My results should be used as a basis for continued research of red foxes and coyotes in and around Lincoln, Nebraska. The data suggested trends that both supported and refuted different aspects of my hypotheses and predictions. The sum of the results would suggest that spatial avoidance is dominant in this system. More time is needed to study the locations of co-occurrence to gain a better understanding of the degree to which temporal avoidance plays a role in red fox and coyote interactions. There are questions that still need to be answered about the interactions of red foxes, coyotes, and humans across urban rural gradients. This study offers a starting point for others to build upon with more robust data sets.

Figures:

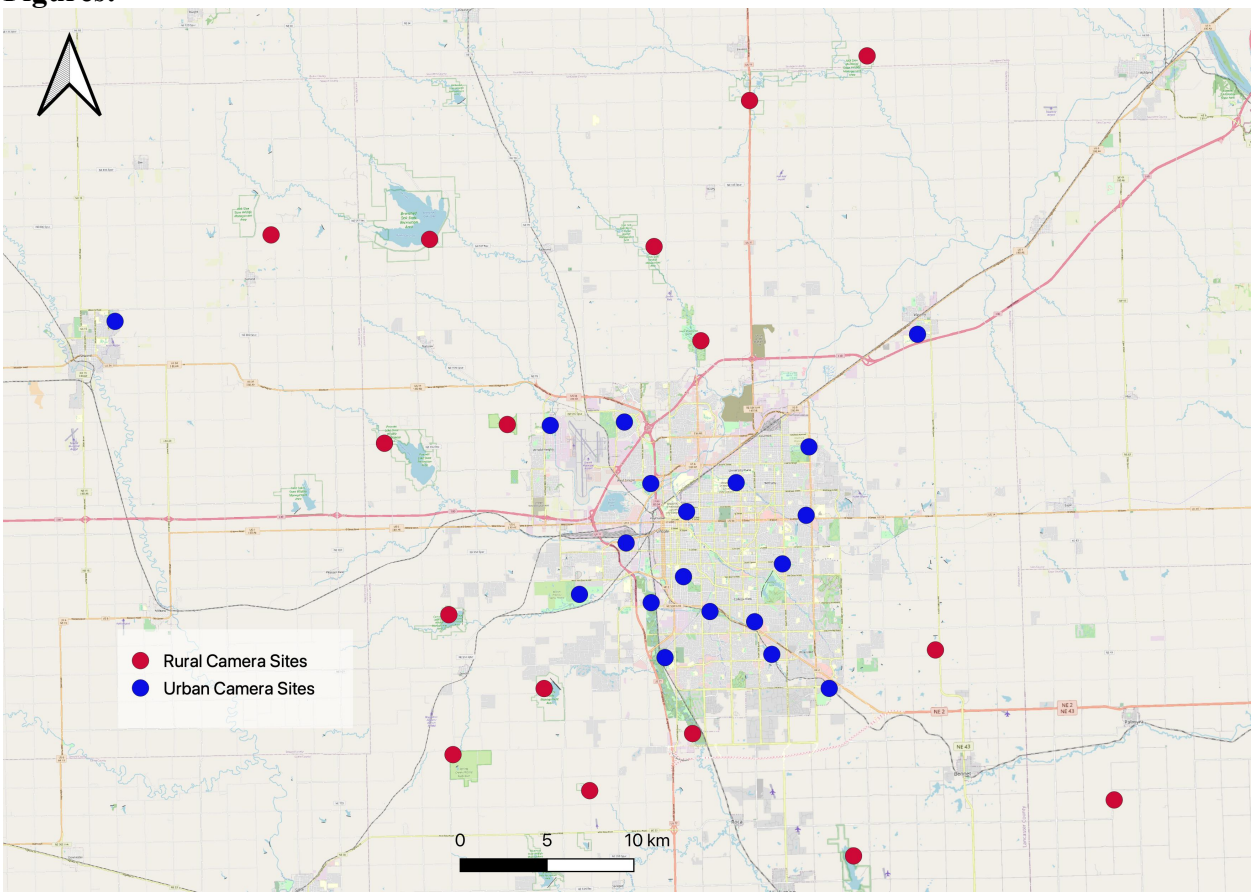

Fig. 1: A map of all camera trap locations. Rural sites n = 16. Urban sites n = 19

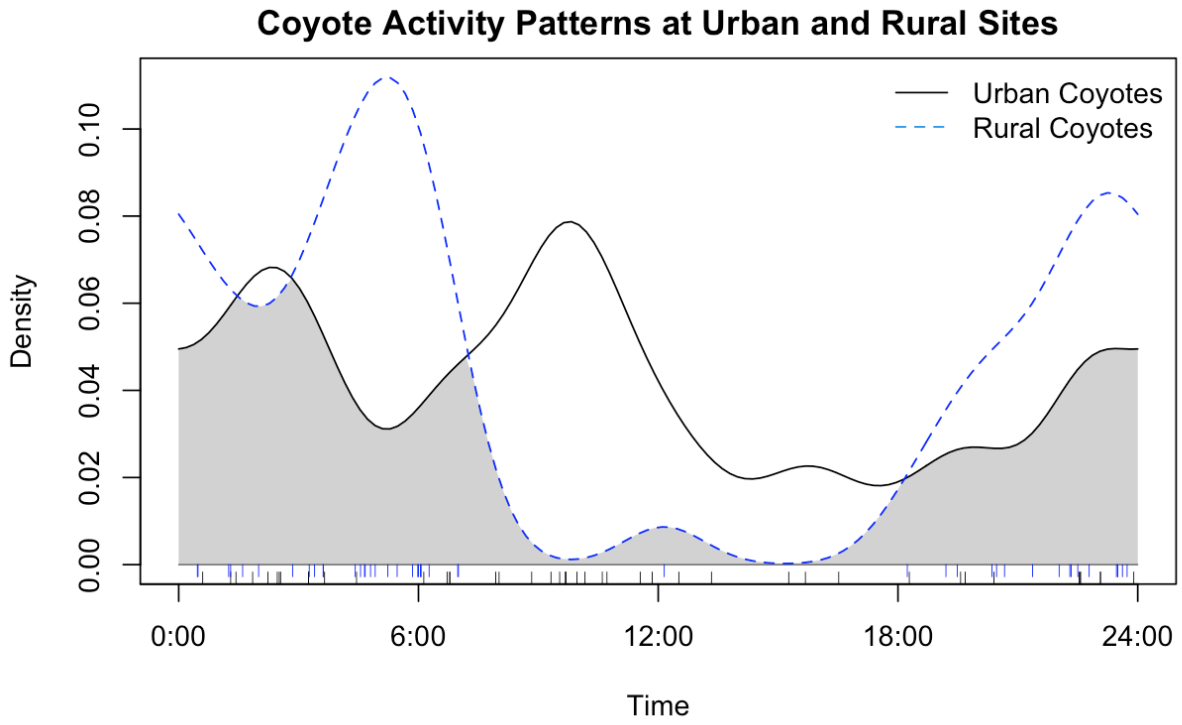

Fig. 2: Overlap of the estimated temporal activity patterns of coyotes captured at urban (n = 45) and rural sites (n = 45). Δ_1 = 0.609 95% CI: 0.464 – 0.734 WT 0.001 < *P* <0.01.

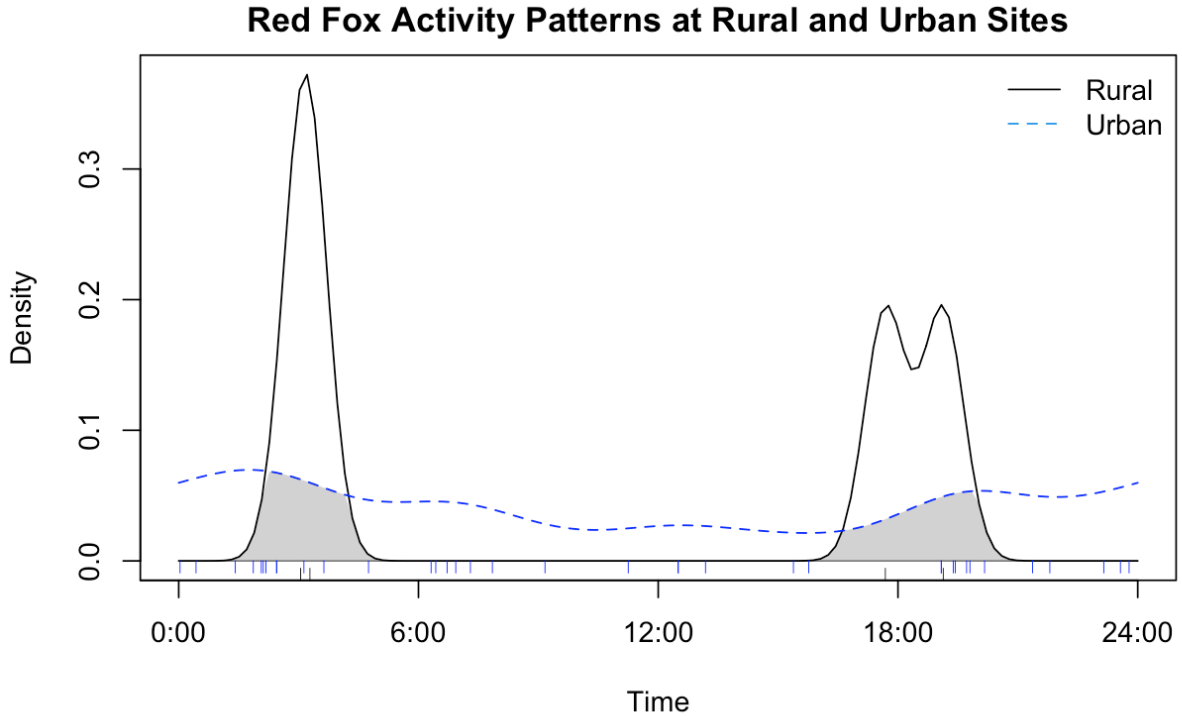

Fig. 3: Overlap of the estimated temporal activity patterns of red foxes captured at urban (n = 76) and rural sites (n = 4). Δ_1 = 0.304 95% CI: 0.125 – 0.577 WT *P* > 0.10.

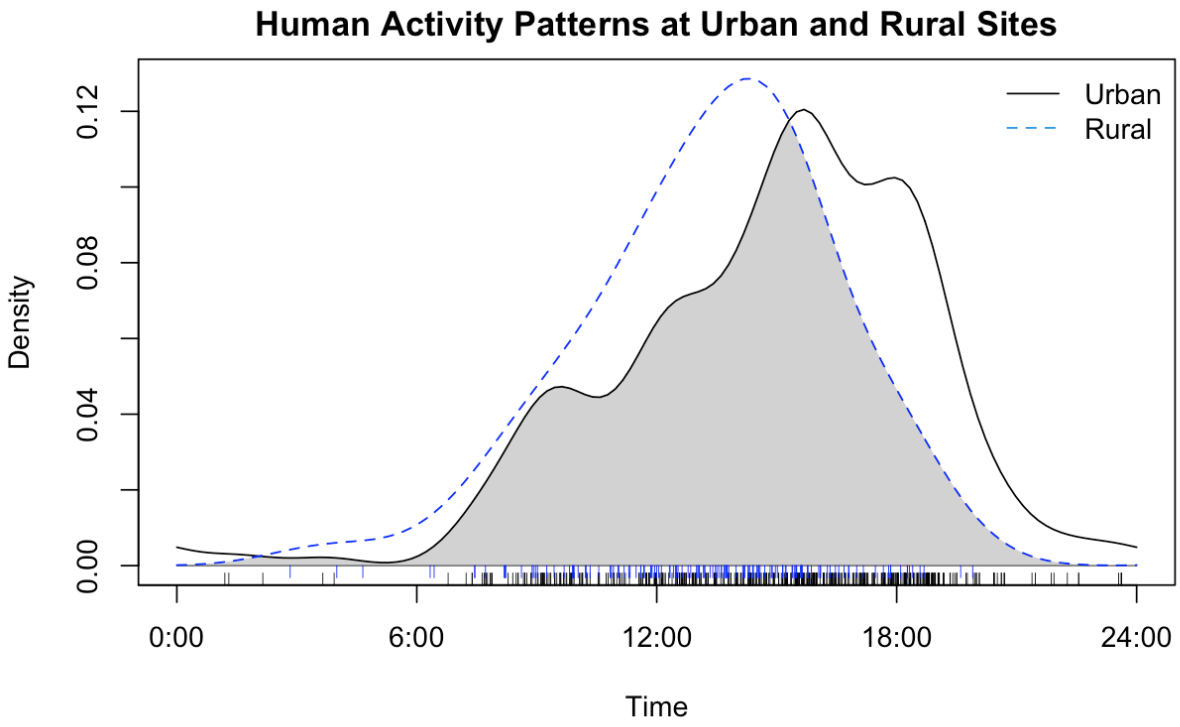

Fig. 4: Overlap of estimated temporal activity patterns of humans captured at urban (n = 484) and rural sites (n = 156). Δ_1 = 0.772 95% CI: 0.699 – 0.846 WT $P < 0.001$.

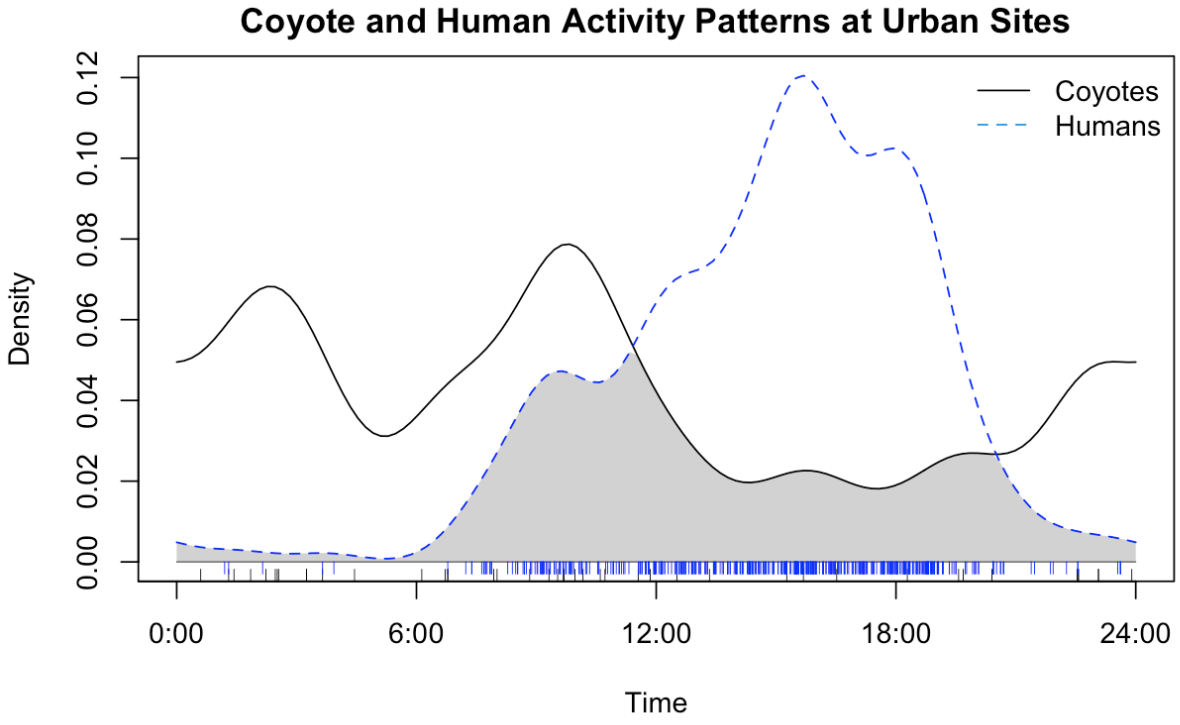

Fig. 5: Overlap of estimated temporal activity patterns of coyotes (n = 45) and humans (n = 484) captured at urban sites. Δ_1 = 0.446 95% CI: 0.336 – 0.556 WT $P < 0.001$.

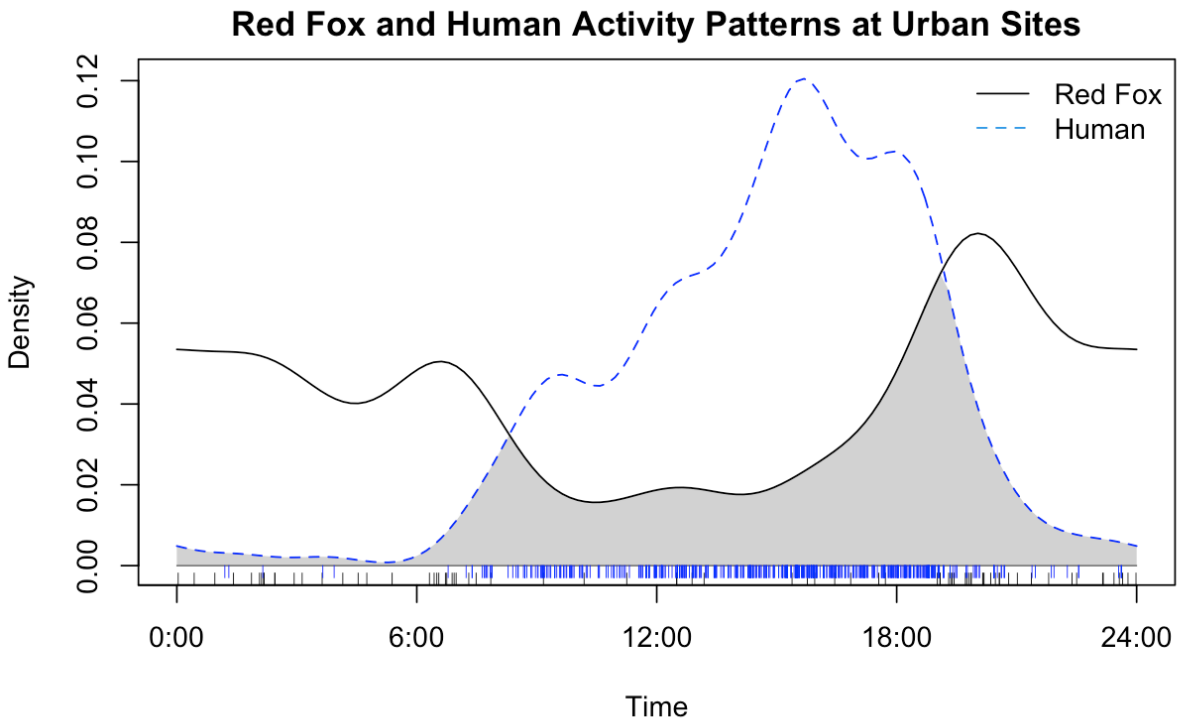

Fig. 6: Overlap of estimated temporal activity patterns of red foxes (n = 76) and humans (n = 484) at urban sites. Δ_1 = 0.426 95% CI: 0.326 – 0.516 WT $P < 0.001$.

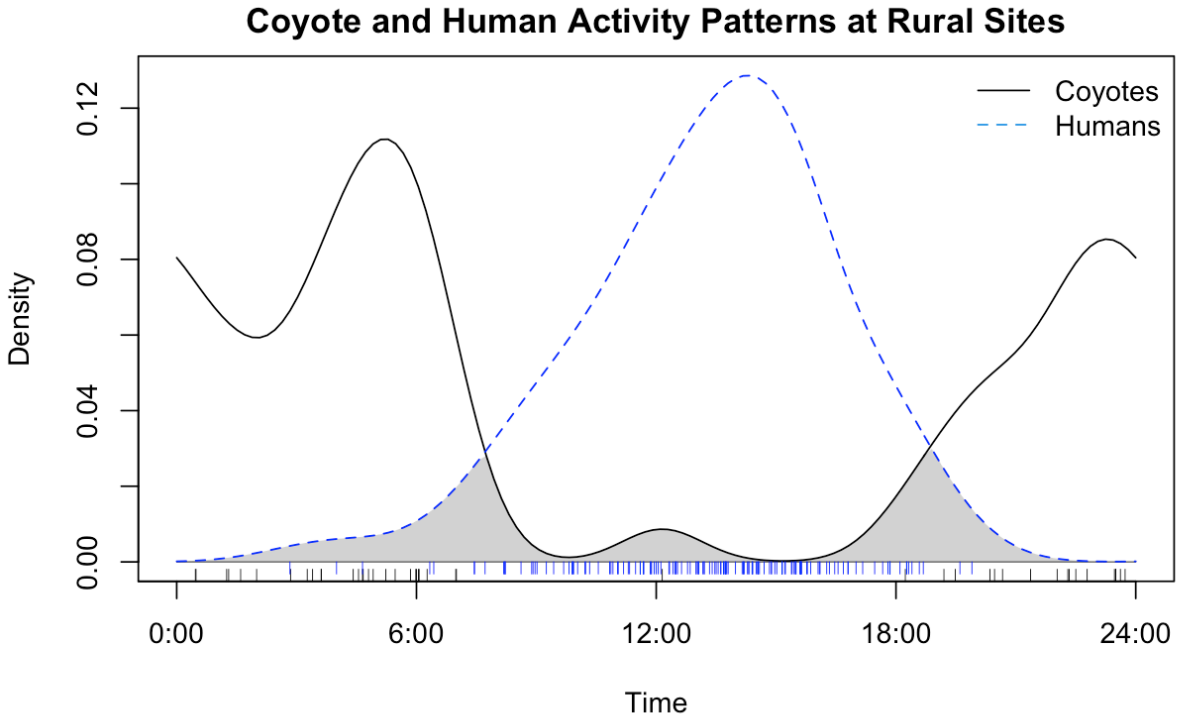

Fig. 7: Overlap of estimated temporal activity patterns of coyotes (n = 45) and humans (n = 156) at rural sites. Δ_1 = 0.157 95% CI: 0.081 – 0.242 WT $P < 0.001$.

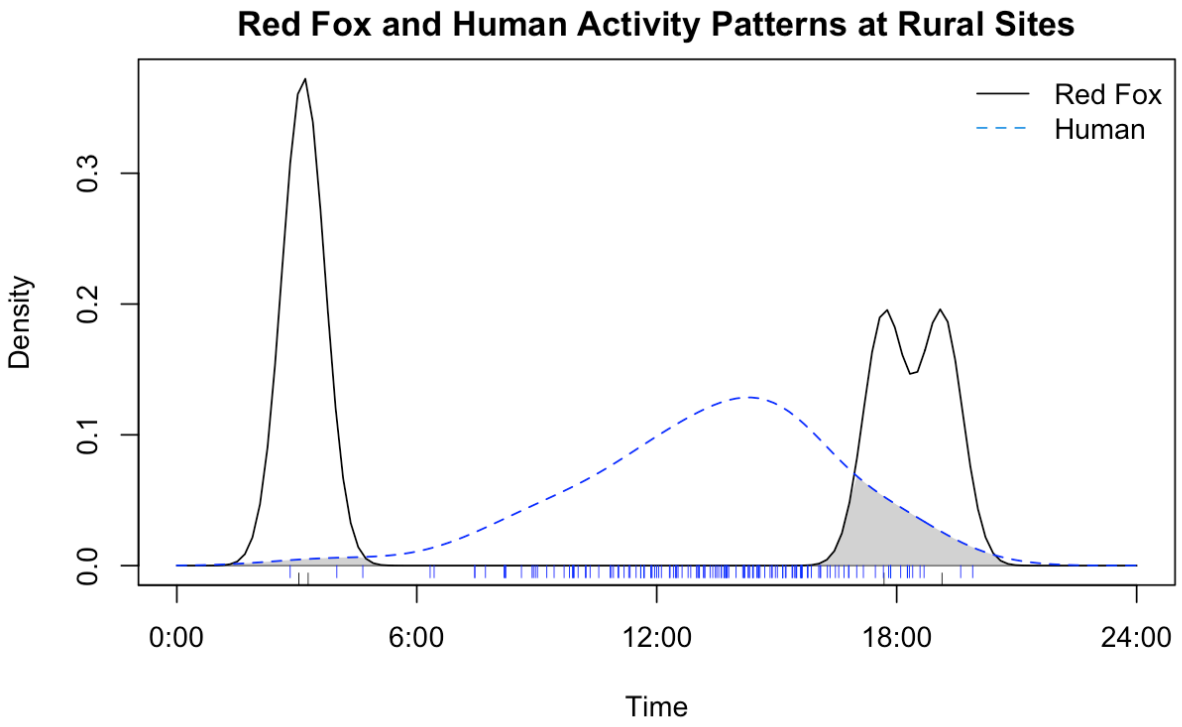

Fig. 8: Overlap of estimated temporal activity patterns of red foxes (n = 4) and humans (n = 156) at rural sites. Δ_1 = .149 95% CI: 0.017 – 0.304 WT $0.01 < P < 0.05$.

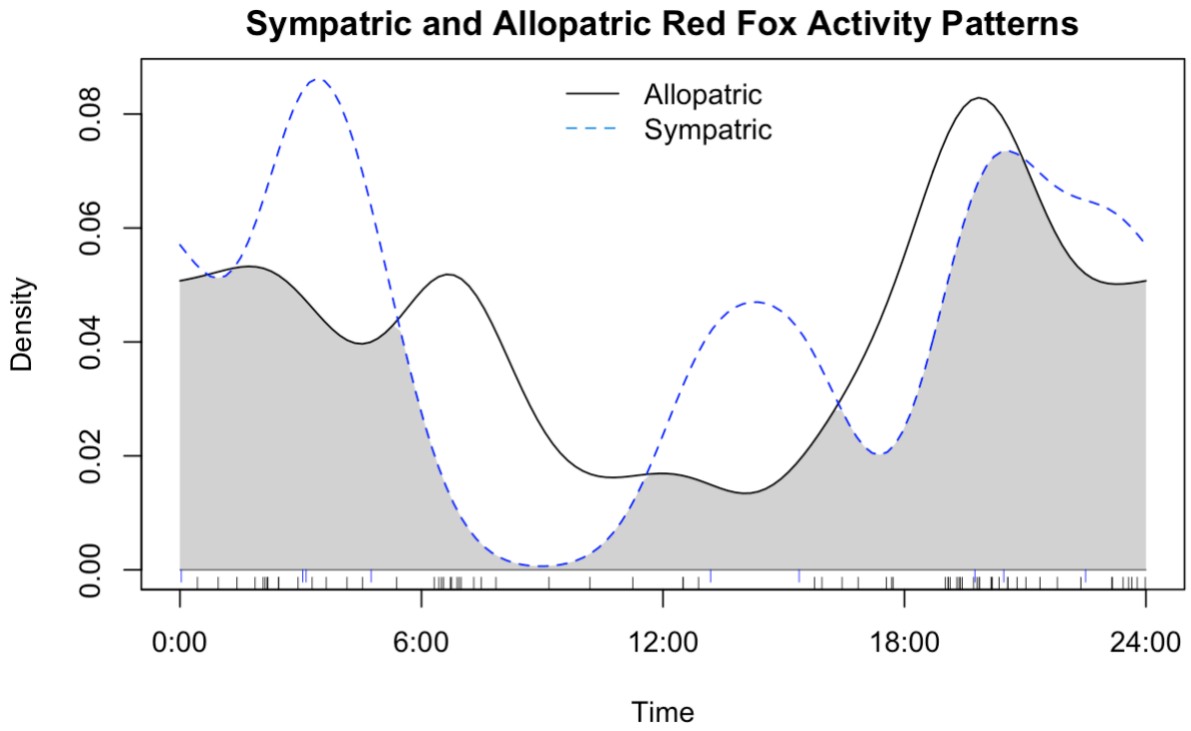

Fig. 9: Overlap of estimated temporal activity patterns of red foxes sympatric with coyotes (n = 9) and red foxes allopatric with coyotes (n = 71). Δ_1 = 0.745 95% CI: 0.528 – 0.933 WT $P > 0.10$

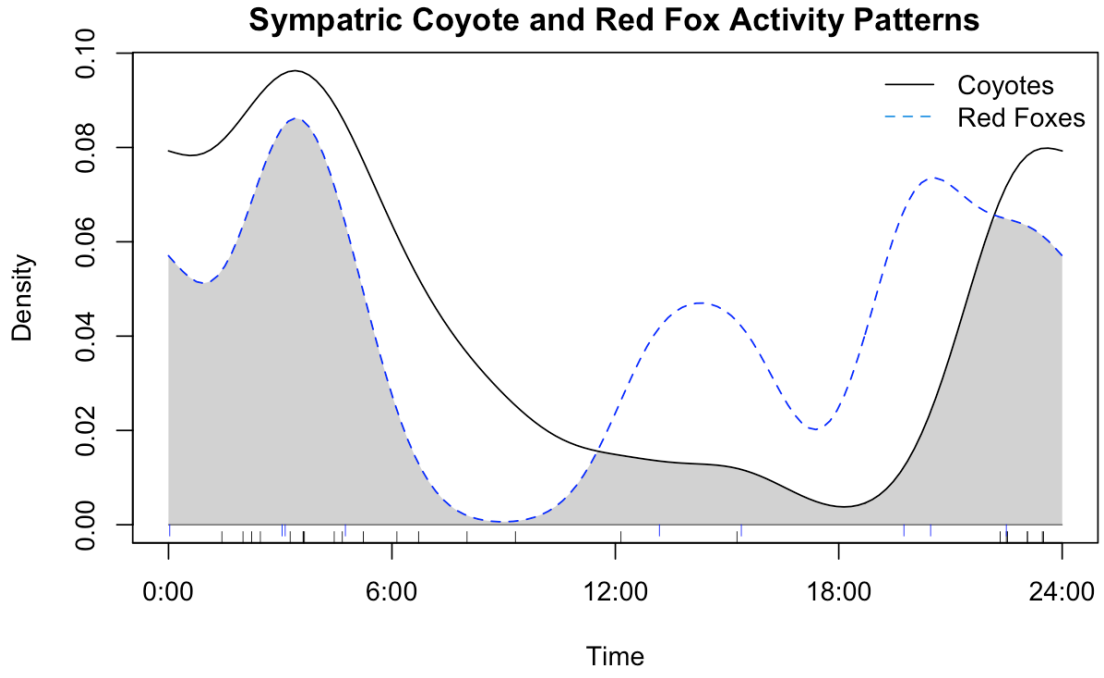

Fig. 10: Overlap of estimated temporal activity patterns of red foxes (n = 9) and coyotes (n = 24) when captured at the same camera location. Δ_1 = 0.689 95% CI: 0.449 – 0.892 WT $P > 0.10$.

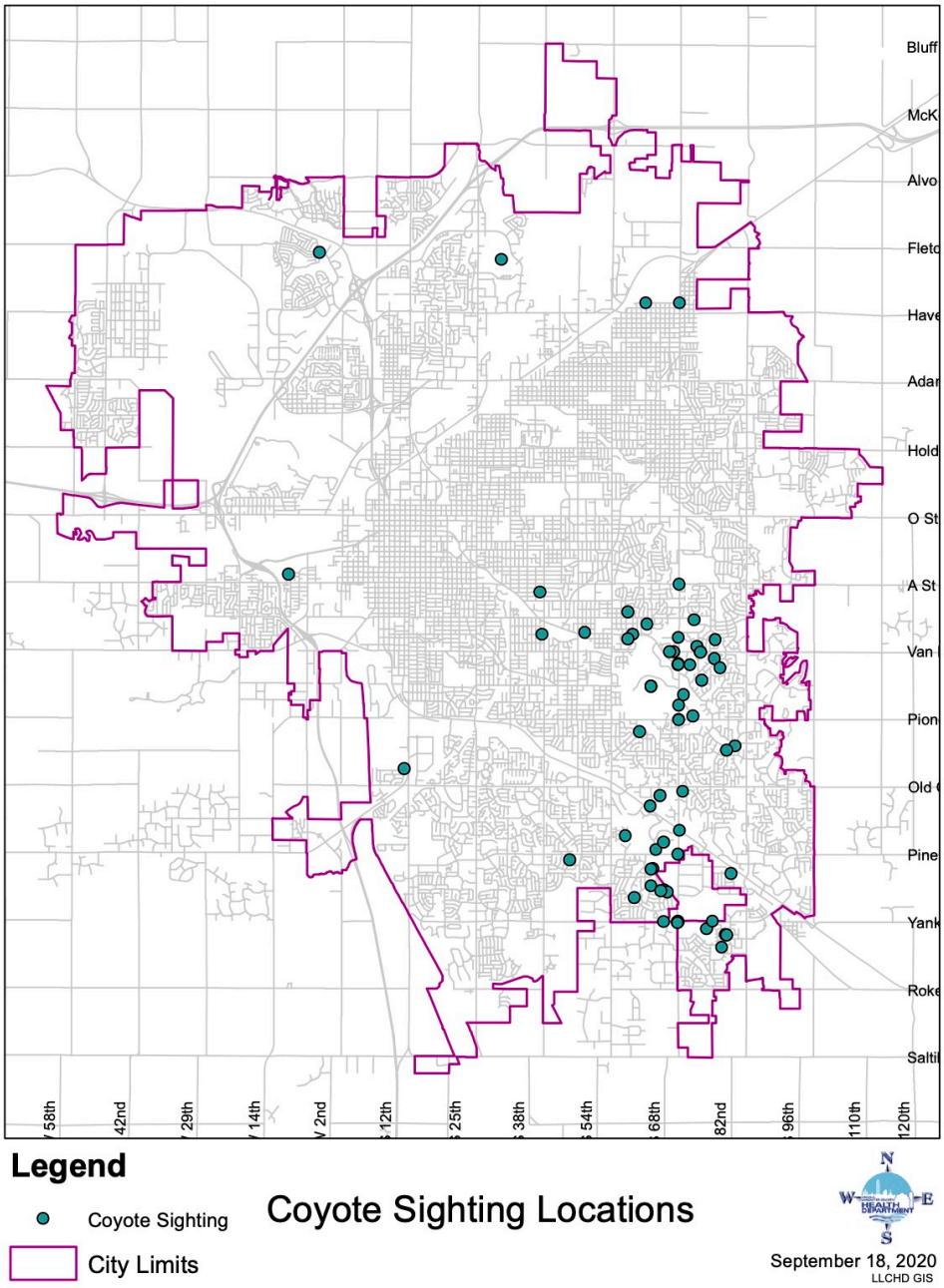

Fig. 11: Map of calls reporting coyote sightings. Provided by Lincoln Animal Control 2020

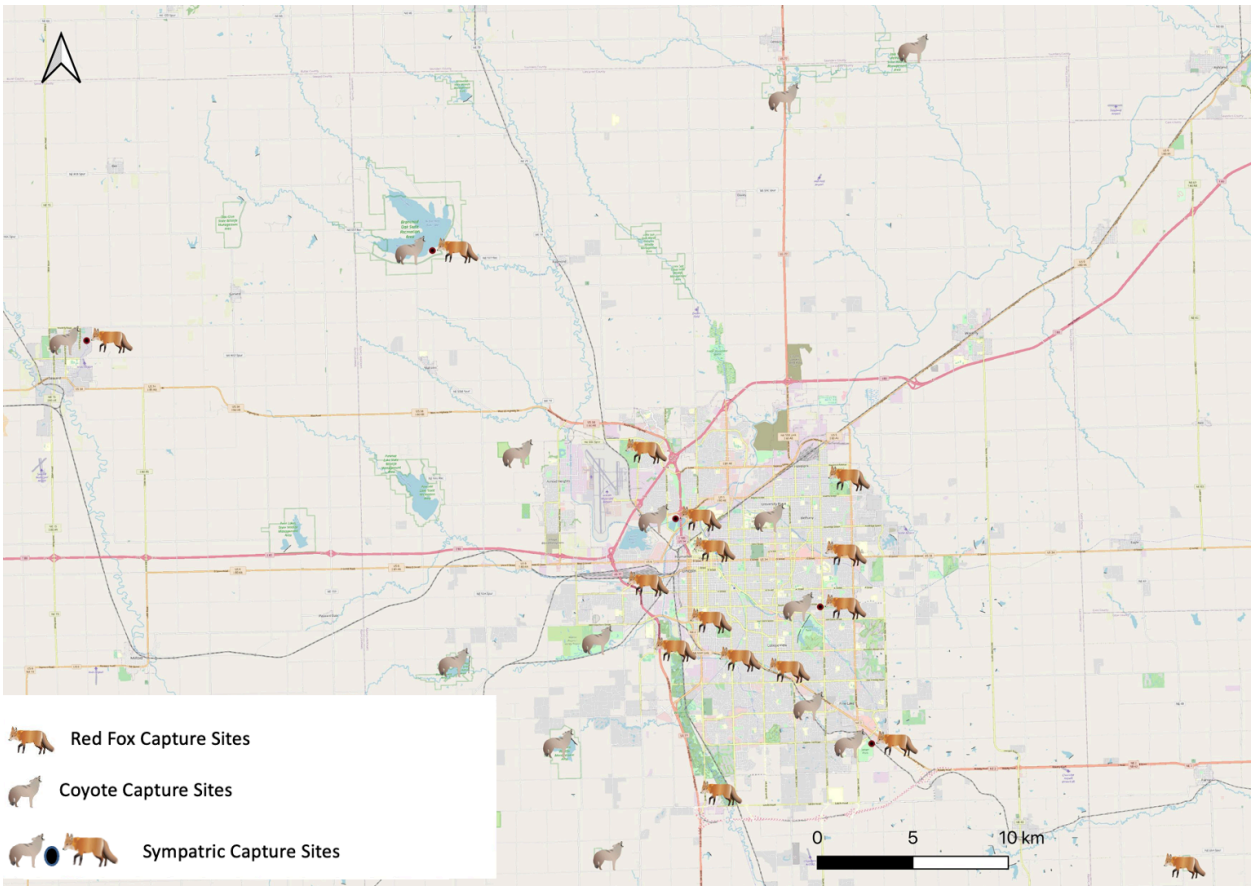

Fig.12: A map separating camera locations based on what animal was captured there. Red fox capture sites (N = 11). Coyote capture sites (N = 10). Sympatric capture sites(N = 5).

Model	# of Parameters	AICc	ΔAICc
Urban	1	73.606	0
Urban + Coyote	2	76.817	3.211
Null	0	80.144	6.538
Coyote	1	80.771	7.165

Table 1: AICc table for the four constructed occupancy models.

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